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Testing the Climatic Variability Hypothesis with coastal and inland populations of Mimulus guttatus and implications for these populations under climate change

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Testing the Climatic Variability Hypothesis with coastal and inland populations of *Mimulus guttatus* and implications for these populations under climate change

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To my friend Kendra Chan who inspired me as a researcher and naturalist, and who I wish so much that I could share this work with

Abstract

How climate shapes the niche of a species is a core interest in evolution and ecology. Research on the evolution of climatic niches can inform us on the historical relationship between organisms and their climate, and, in an era of great environmental change, what that relationship may look like in the future. In this study, I tested an essential idea in the history of climate niche research, the Climatic Variability Hypothesis, by comparing the thermal niche breadth of coastal and inland populations of *Mimulus guttatus*. Using thermal performance results from this experiment, I also forecasted how the suitability of thermal habitat may change for these populations. Unexpectedly, coastal and inland populations did not differ in thermal niche breadth. All populations possess relatively wide performance curves. However, I found other interesting differences in their thermal performance curves that are deserving of further research. Because populations differed little in their performance curves, they all show similar responses to temperature increases. These increases are actually projected to bring more favorable thermal conditions for all populations. However, this is only assuming that plants have plentiful water. Drier conditions caused by climate change may outweigh benefits from warmer temperatures. Of course, measuring and quantifying the climatic niche of an organism and predicting its future are complex tasks. I introduce what I hope are improvements, if only minor, to methods that have previously been used.

Introduction

How climate shapes the niche of a species is a core interest in evolution and ecology. Climate determines range boundaries across plants and animals (Moritz et al. 2008; Peck et al. 2009; Ettinger et al. 2011). Especially for plants, which cannot move after establishing, temperature often sets the physiological limits of where an organism can exist (Alvarez-Uria and Körner 2007; Normand et al. 2009). One way to describe thermal limits is by defining the niche breadth of an organism. Niche breadth can be simply thought of as the range of conditions under which an organism can maintain or increase population size (Sexton et al. 2017; Carscadden et al. 2020). Fitness likely varies across this range, with the greatest fitness at some optimal condition and reduced fitness towards the extremes (Lynch and Gabriel 1987). Niche breadth itself has been the subject of much research in ecology, evolution, and conservation, spanning topics like community assembly, species distributions, speciation, and invasive species (Carscadden et al. 2020). In response to climate change, researchers have studied the thermal niches of taxa to better understand how they will respond (Angert et al. 2011; Sunday et al. 2012; Shah et al. 2017; Peterson et al. 2018). An organism's thermal niche breadth has important implications for its ability to persist under climate change, since organisms with wider thermal niche breadths may be able to better handle temperature increases. In this study, I test an essential idea in the history of niche breadth research, the Climatic Variability Hypothesis (CVH). I also discuss thermal niche research, especially that related to the CVH, which has primarily been conducted in ectothermic animals. Though research on animals is relevant, there are important distinctions between how thermal limits are studied in plants and animals. Last, I touch on using thermal performance to predict responses to climate change.

The Climatic Variability Hypothesis

I define the CVH simply — that organisms should be adapted to handle the climatic conditions they regularly experience so that organisms in more variable climates have wider thermal niches. This essential idea has been featured in the literature for some time. Allee et al. (1949) discussed research in which the cold hardiness of an insect was positively correlated with the temperature fluctuations of the insect's habitat. Dobzhansky (1950) compared the climate of tropical and temperate environments, citing the relatively stable climate of the tropics to argue that the biotic environment played a greater role in the evolution of tropical organisms, whereas the abiotic environment was more important in temperate areas. However, the origin of the CVH is usually connected to two other researchers: Janzen (1967) and Stevens (1989).

Janzen provided a far-reaching extension of the CVH. Slightly rebutting Dobzhansky, he proposed that because tropical organisms experience more uniform thermal regimes and may be adapted to a more narrow range of temperatures, mountains could pose a greater barrier to dispersal in the tropics (Janzen 1967). Janzen's idea has been well studied and verified over the past fifty years (Ghalambor et al. 2006; Smith 2018), but it also took on a life of its own. In his paper, Janzen stated, "This is not an attempt to explain tropical species diversity" (Janzen 1967). Yet, Janzen's idea has clear implications for tropical species diversity. Smaller climatic niches and limited dispersal could mean a greater number of species can accrue in a given area. Researchers on this topic, citing Janzen as inspiration, have shown that narrower thermal tolerances in the tropics drive higher aquatic insect diversity along mountains (Shah et al. 2017; Polato et al. 2018).

Stevens provided a similar, but distinct, extension of the CVH. He proposed Rapoport's Rule — that species' geographic range sizes increase from the equator to the pole — and used the CVH to support this rule (Stevens 1989). He reasoned that if temperate species have wider

climatic niches, they should be able to occupy a larger geographic range than tropical organisms. Rapoport's Rule has been controversial and not well supported, largely because there is not always an increase in climatic variability with an increase in distance from the equator (Rohde et al. 1993; Gaston et al. 1998; Gaston and Chown 1999). Yet, the underlying idea that climatic variability can affect range size has received support (Letcher and Harvey 1994; Pintor et al. 2015).

Studies on the CVH always cite Janzen or Stevens, and usually both. Interestingly however, neither of these researchers used the phrase "climatic variability hypothesis" in their seminal works, and Stevens only used the phrase "seasonal variability hypothesis" in later work (Stevens 1996). The first use of a distinct term in the literature for this idea was Letcher and Harvey's (1994) work on Rapoport's Rule. They describe the CVH as an explanation for Rapoport's rule:

> "One proposed explanation for Rapoport's rule is the climatic variability hypothesis. The argument runs that an individual animal at the polar end of a continent experiences a much wider range of climatic conditions than one at the equatorial end. Accordingly, more temperate species cannot specialize on a narrow set of climatic conditions, unlike tropical species, and are therefore selected to be generalists. Generalists are not restricted to a particular habitat type and consequently have large geographical ranges. Tropical species never experience the climatic variation of the temperate species, are much more specialized, and have smaller ranges. Generalists are more likely to overlap in their niche requirements, so competitive exclusion reduces diversity nearer the poles." (Letcher and Harvey 1994)

Letcher and Harvey explicitly tied the CVH to Rapoport's Rule and comparisons of tropical and temperate organisms. I provide this information to highlight the convoluted history of the CVH. Because of this, its definition is often entangled with the ideas of Janzen and Stevens. Even recently, researchers provide similar definitions for the CVH (Polato et al. 2018). Yet the CVH does not need to be constrained in this way. For example, Wooliver et al. (2020) describe it as the idea that "populations inhabiting regions that are climatically stable should evolve narrower climatic tolerances relative to those from climatically heterogeneous areas." This definition is analogous to the one I provided earlier. It explains the essential principle underlying Janzen's and Stevens's propositions but deals only with how climatic variability can directly influence organisms.

Using Wooliver et al.'s definition, researchers have found mixed support for the CVH (Molina-Montenegro and Naya 2012; Pintor et al. 2015; Gutiérrez-Pesquera et al. 2016; Shah et al. 2017; Janowiecki et al. 2019; Pallarés et al. 2019; Sentinella et al. 2020; Wooliver et al. 2020). Most of these studies still focused on tropical-temperate comparisons or latitudinal gradients (Molina-Montenegro and Naya 2012; Gutiérrez-Pesquera et al. 2016; Shah et al. 2017; Janowiecki et al. 2019; Sentinella et al. 2020), though there are a few exceptions (Pintor et al. 2015; Pallarés et al. 2019; Wooliver et al. 2020). Almost all research in this area has been conducted on animals, and usually ectotherms. Only a handful of studies have focused on plants. In the first study to test the CVH using plants, researchers found that individuals of the invasive *Taraxacum officinale* collected from higher latitudes displayed greater plasticity in a number of functional traits between two temperature treatments (Molina-Montenegro and Naya 2012). In another study, researchers found no difference in the thermal germination niches of tropical and temperate plants (Sentinella et al. 2020). A recent study using similar methods as this thesis

found a significant positive relationship between thermal performance breadth and temperature seasonality in populations of *Mimulus cardinalis* (Wooliver et al. 2020). Interestingly, in this study, latitude was not correlated with seasonality, as is often assumed, yet the CVH held true. If we are to understand how applicable the CVH is, we must study it thoroughly across taxa and habitat types.

An implication of the CVH is a specialist-generalist tradeoff. If organisms from less variable environments have evolved smaller niche breadths, we may expect these organisms to perform especially well within this small range of conditions compared to organisms from more variable environments (Gilchrist 1995; Angilletta et al. 2003). This is attributed to energetic costs to generalists from maintaining performance over a wider range of conditions (Somero 1995). I look for evidence of this trade-off in my study, as well.

Thermal Tolerance and Thermal Performance

Thermal tolerance research, especially that related to the CVH, has long been conducted on ectothermic animals (Cowles and Bogert 1944; Lutterschmidt and Hutchison 1997). Researchers measure either the lethal thermal limits, which are the temperatures at which a certain percentage of organisms die during a fixed exposure time, or critical thermal limits, which are the mean temperatures at which organisms lose essential motor function (Sunday et al. 2011). Tolerance breadth is then calculated as the difference between the upper and lower limit. Likely due to the relative ease of measuring critical thermal limits in ectothermic animals, much previous work has used them, especially for the CVH (Lutterschmidt and Hutchison 1997; Shah et al. 2017; Polato et al. 2018). They provide clear temperature points at which the fitness of an organism will certainly fall to zero. However, for endotherms and plants, it is not easy or always possible to determine a distinct temperature at which these organisms lose an essential function.

Early studies on the thermal niche of plants measured the photosynthetic yield of leaf tissue under different temperatures (Loik and Harte 1996). More recently, researchers have used growth chamber experiments in which they measure growth or seed production across a range of temperatures (Angert et al. 2011; Sheth and Angert 2014; Lacher and Schwartz 2016; Peterson et al. 2018; Wooliver et al. 2020). These methods allow researchers to build thermal performance curves, which not only describe where performance falls to zero, but how the organism performs across the whole range of temperatures (Huey and Stevenson 1979; Huey and Kingsolver 1989; Angilletta 2006). Interestingly, here niche breadth can be measured in two different ways — tolerance breadth or performance breadth (Fig. 1). Tolerance breadth can again be measured as the difference between the upper and lower points at which performance falls to zero. Instead, researchers often measure the performance breadth — the width of the curve at a given percentage of the curve's maximum (Huey and Kingsolver 1989; Wooliver et al. 2020). Especially when fitness is not directly measured, calculating performance breadth allows one to measure the range of temperatures at which an organism is more likely to survive and reproduce (Huey and Stevenson 1979). Performance breadth can also be compared across multiple points (e.g. 50% and 80% of the maximum) to ensure that results qualitatively agree (Sheth and Angert 2014; Wooliver et al. 2020).

Despite the clear logic of measuring performance breadth, it is not analogous to tolerance breadth (Huey and Stevenson 1979). In fact, it forces one to reconsider old arguments about the use of critical thermal limits: that critical thermal limits only deal with extremes and not the temperatures organisms regularly experience (Lutterschmidt and Hutchison 1997). However, rare extreme temperatures in variable environments can dominate selection on thermal tolerances (Kingsolver and Watt 1983). There is evidence that the temperature limits of some organisms are

more important than their temperature optima in determining where those organisms can live (Overgaard et al. 2014; Shocket et al. 2020). As with much in evolution and ecology, the influence of thermal limits versus thermal optima likely varies across taxa, time, and space. One can imagine that greater variability could select for greater tolerance breadth, greater performance breadth, or both. Studies have found support for the CVH using performance breadth or tolerance breadth (Shah et al. 2017; Wooliver et al. 2020), but no one has explicitly compared both measures. In my study, I make that comparison.

Predicting Responses to Climate Change

Until relatively recently, researchers treated species as monolithic units when forecasting responses to climate change — potentially oversimplifying predictions (Thuiller et al. 2008). This is due in part to the primary method used: species distribution models. These models use correlations between occurrence records and historical climate to estimate a species' climate niche and predict future habitat suitability (Peterson 2003; Franklin 2010). Species distributions models have been widely used because occurrence data is easily available and there are relatively few obstacles to using relevant software (Peterson et al. 2019). Though these models are informative, researchers have increasingly recognized the limits of species distribution models. Primarily, because these models usually use species wide occurrence records to estimate a species-wide climatic niche, they ignore important intraspecific variation (Peterson 2020). Variation in climate across a species range likely selects for divergent environmental niches (Hereford 2009; Franks et al. 2014). This means not only that populations of one species may respond differently to environmental change, but that widespread species could be vulnerable across their range (Angert et al. 2011; Schwartz 2012). Because widespread species were thought to have large environmental niches, they are usually not of conservation concern. However, Peterson et al. (2018) found that populations of *Silene acaulis* from Alaska to New Mexico

exhibited opposing responses to climate change and are all sensitive to warming. Research on *Mimulus guttatus* has shown that though it is widespread, individual populations do not have thermal niches to match the whole range (Lacher and Schwartz 2016).

Though researchers have recently attempted to account for intraspecific variation in species distribution models, the use of occurrence records limits the strength of these studies. Researchers can compare if intraspecific groups occupy different climatic niches but cannot speak to differences in performance across groups because occupation could be confounded by a number of other abiotic or biotic conditions (Peterson et al. 2019). Mechanistic models offer an alternative to species distribution models that can more robustly incorporate intraspecific variation. Mechanistic models use knowledge on individual performance that is linked to climate to predict responses to climate change. If researchers measure multiple populations, they can compare how differences in population performance may impact responses to climate change. Because more work is required to collect this knowledge, mechanistic models are relatively rare. In a review of forecasts that incorporate intraspecific variation, only four studies used mechanistic models compared to eighteen for species distribution models (Peterson et al. 2019). In my study, I use a mechanistic model to understand how climate change will affect thermally suitable habitat for coastal and inland populations of the same species.

The CVH, the Coast, and Climate Change

The CVH has new relevance as researchers have realized its implications under climate change. Aquatic insects from the tropics are more sensitive to climate change because their thermal niches are so small, despite rates of temperature increases being lower in the tropics than in temperate areas (Shah et al. 2017; Polato et al. 2018). We must wonder, are there organisms from other stable climates that are especially sensitive to climate change?

Along the California coast, climate change is expected to increase temperatures and decrease fog cover, leading to warmer, drier habitat (Johnstone and Dawson 2010; Kawai et al. 2018). Research into how plants may respond to these conditions has focused primarily on reductions in fog since this is an important and unique component of coastal California communities (Fischer et al. 2009; Johnstone and Dawson 2010). Yet, coastal plants may be especially sensitive to changes in temperature and, consequently, even more impacted by climate change. The San Francisco Bay Area provides a unique place to test the CVH and its implications under climate change. Coastal areas generally experience smaller temperature fluctuations than inland areas due to marine influence, and the coast near the San Francisco Bay, as noted by Janzen (1967), is especially stable because it is backed by low mountain ranges. In fact, coastal California has temperature fluctuations more similar to a coastal tropical site than to an inland California site 3 km away (Fig. 2). According to the CVH, we would expect coastal organisms to have more narrow thermal niches and may therefore be more sensitive to climate change.

Coastal species often occupy restricted ranges along the coast, and climate change will decrease suitable habitat to an even more narrow band (Dolan and Walker 2006). Not only are coastal communities expected to face higher mean temperatures, but reductions in fog will also lead to greater fluctuations in temperature (Torregrosa et al. 2014). If coastal species have especially narrow thermal niche breadths, they may lose suitable habitat at a greater rate than expected. Furthermore, coastal species often occupy unique habitat that is patchily distributed along rocky outcrops or bluff faces. These species may be limited in their ability to disperse to newly suitable habitat as climate changes. We must understand the threats coastal species face in order to appropriately direct conservation efforts towards such species.

For my thesis, I studied the native widespread wildflower *Mimulus guttatus* to test the CVH between coastal and inland environments. I surveyed populations that varied in thermal regimes and distance from the coast and selected six populations for my study. I collected seed from the field, then grew and crossed a greenhouse generation of plants to produce seeds with reduced parental effects. With this seed, I performed a thermal performance experiment. For this performance experiment, I developed a computational workflow to more easily measure growth in leaf area and calculate relative growth rate as a measure of performance. I tested the CVH with the resulting thermal tolerance and performance data. Lastly, I estimated thermal habitat suitability under current and future climate conditions by incorporating the thermal performance data into a mechanistic niche model.

Methods

Study Species

Mimulus guttatus is an herbaceous plant whose range spreads latitudinally from Alaska to northern Mexico and longitudinally from the Pacific Coast to the Rocky Mountains (Baldwin et al. 2012). Across this range, *M. guttatus* occupies diverse climatic habitats, from the coast to high-elevation montane habitat (Calflora 2014). *M. guttatus* exhibits several, unique ecotypes and has long been considered a species complex, causing uncertainty around the taxonomic placement of different ecotypes (Vickery 1978). There is currently controversy over the taxonomy of this group (Lowry et al. 2019*b*; Nesom et al. 2019). A recent revision placed most Western North American species of *Mimulus* into two different genera: *Erythranthe* and *Diplacus* (Barker et al. 2012). This same revision also elevated the coastal perennial ecotype and inland annual ecotype of *M. guttatus* each to their own species, *E. grandis* and *E. microphylla* respectively, while maintaining inland perennials as *E. guttata* (Barker et al. 2012; Nesom 2012). However, recent molecular analyses have shown all three ecotypes experience substantial gene

flow. In fact, outside of a chromosomal inversion that is associated with life history, there is no genetic structure among ecotypes (Oneal et al. 2014; Twyford and Friedman 2015; Twyford et al. 2020). Here, I treat the different ecotypes as within the broader circumscription of *Mimulus guttatus sensu lato* (Grant 1924). Whatever the current taxonomy of the group, the principles of my thesis are the same — I studied related populations to better understand how climate has shaped their thermal niches and how they may respond to climate change.

Mimulus guttatus is an excellent species for this study. It grows well in controlled environments, meaning it is very amenable to thermal performance experiments (Wu et al. 2008). Not only does this species live in both coastal and inland habitats, but there are distinct ecotypes associated with these habitats. There is plentiful evidence of local adaptation in studies comparing coastal perennial and inland annual ecotypes (Lowry et al. 2008, 2019*a*; Popovic and Lowry 2020). Coastal populations have adaptations to handle saltwater and increased herbivore pressure (Lowry et al. 2019*a*; Popovic and Lowry 2020). Though this does not necessarily mean that coastal populations have different thermal niches, it does show that these populations are at least somewhat adapted to their unique environment. It is important to note here that I only studied perennial populations. Since annual plants experience only a portion of the climate at their given location, this could confound studies of their thermal niches. This is especially true in a study about climatic variability, since annual plants would likely experience a smaller amount of variability than perennial plants in the same location. Though this offers interesting avenues of research, for the sake of the current study, I focused solely on perennial populations.

Population Selection

During the spring and summer of 2019, I surveyed 37 sites in the San Francisco Bay Area and Mono Lake regions to find suitable study populations. I surveyed sites based on occurrence records from Calflora and iNaturalist. Multiple factors can make it difficult to find suitable

populations. Because *M. guttatus* often grows in seeps, many populations consist of only a few individuals confined to a small seep. Additionally, *M. guttatus* can reproduce vegetatively by stolons, so it can be difficult to identify genetically-unique individuals. Lastly, because flower morphology is superficially similar in a number of closely related *Mimulus* species, many occurrence records for the widespread *M. guttatus* are incorrect identifications of other species (e.g. *M. tilingii* and *M. nasutus)*. Therefore, I searched for true *M. guttatus* populations with enough individuals spread across a wide enough area to collect seed from at least ten, but usually more, distinct maternal plants. I selected six populations to include in the experiment, three coastal populations and three inland populations (Table 1; Fig. 3)

Seed Collection

During the late summer of 2019, I collected seed from the six study populations. As mentioned, populations grow in small seeps or creeks, where a linear path can be followed. At each site, I followed along a predetermined path, collecting from individuals that were at least 1.5m apart to avoid collecting from siblings or clonal replicates. I also made sure to collect from across the entire spatial area of the population to maximize genetic diversity in my collections. Per permit restrictions, I collected no more than 5% of seed on each plant and no more than 5% of seed across the population. I stored seed in the lab until planting. See Table 1 for collection counts of each population.

Historical Climate Data

To understand the recent climatic history experienced by my study populations, I downloaded downscaled hourly temperature data using the *microclima* (version 0.1.0) and *NicheMapR* (version 3.0.0) packages (Kearney et al. 2020). These data span from 1979 to present. To verify the accuracy of these downscaled data, I installed two temperature loggers (HOBO 64k Pendant UA-001-64) at each site during the summer of 2019. I set up the loggers at

~.5m height inside a shelter (HOBO Solar Radiation Shield RS1). The shelter protects the logger from sunlight while allowing plentiful airflow so that recordings accurately reflect air temperature. The loggers recorded hourly. I calculated temperature variation as the standard deviation of all hourly temperature recordings for a given site and time period. Temperature seasonality can also be calculated as the mean range between the warmest and coldest temperatures of each year (Wooliver et al. 2020). This calculation of seasonality was highly correlated with the standard deviation (.999), so I just used standard deviation.

Controlled Crosses

I generated controlled crosses in order to produce seed with reduced parental effects. *M. guttatus* has a sensitive stigma that closes when touched, making it unreceptive to pollen (Friedman et al. 2017). Additionally, the stamens are attached to the corolla, which can be easily removed. These two traits make emasculating and crossing *M. guttata* flowers relatively simple. In January 2020, I cold stratified seed from each maternal family in a microcentrifuge tube in a .15% agar solution. I stored seeds in the dark at 4ºC for 1 week, then planted in 4.5" pots with SunShine Mix #4 (Sun Gro Horticulture; Agawam, MA). I planted two pots for each maternal family, and planted 5-10 seeds per pot to ensure at least one individual would germinate. If multiple individuals germinated in a pot, I thinned to the centermost individual within the first two weeks after germination. I placed pots in trays, which allowed me to bottom water the pots. I bottom-watered once a week, except during especially warm periods in which case I bottom-watered twice a week. Ideally, I would have used the grow lights to expose plants to long days (16 hours) to trigger flowering at the same time across populations. However, COVID-19 shutdowns reduced my access to the greenhouse and my ability to work with others to learn how to use the greenhouse equipment. So instead, I let the plants grow and flower naturally. They flowered from May through October 2020, so I regularly performed crosses during this time. I

randomly paired individuals within each population, with one individual serving as the sire and one serving as the dame. I made sure that pairs did not include two individuals from the same maternal family and that no pair had individuals from the same two maternal families as another pair. In total, I produced seventy-seven full-sibling families. See Table 1 for numbers for each population.

Thermal Performance Experiment

Using seed from the controlled crosses, I performed a thermal performance experiment by exposing plants to a range of temperature treatments and measuring growth in leaf area over one week. I performed eight temperature treatments: 5, 10, 15, 20, 25, 30, 35, and 40ºC. These temperatures span the range of temperatures regularly experienced by the study populations and performance falls to or near zero at the extremes, allowing me to build thorough performance curves. Because we only have four growth chambers of the same model (Conviron A1000), I staggered treatments into two sets that were one week apart. For each set of treatments, I planted into 50-cell plug trays with SunShine Mix #4. I planted six trays per treatment. I randomly assigned the tray and cell location for each individual when planting. I planted 3-4 replicates per seed family in each treatment; there was not enough space to plant 4 replicates for all families, so I randomly selected which seed families would have a fourth replicate separately for each treatment. After planting, I cold stratified the trays in the dark at 4ºC for one week. After cold stratification, I moved the trays to the greenhouse, misted them well, then covered them with humidity domes for one week. After removing the humidity domes, I misted overhead every day for one week. At the beginning of the fourth week, I bottom-watered with two liters of fertilizer solution (MiracleGro All Purpose Plant Food). During this fourth week, I thinned seedlings to the center-most individual. At the end of the fourth week, I poured off any remaining fertilizer solution, then moved the trays to the growth chambers for temperature treatments. I maintained a

water depth of .5” during the treatment to ensure plentiful water. During the first set of treatments, I performed the 10, 20, 30, and 40ºC treatments. During the second set, I performed the 5, 15, 25, and 35 ºC treatments. I randomly assigned treatments to their given growth chamber.

For each treatment, I set the chamber to maintain its given temperature for the whole week — day and night. I set relative humidity to 25%, though chambers stayed at about 80% humidity during the treatment. I set the day length to 10 hours, with a light intensity of 2 (433 µmol/m²/sec at 6 in). Similar studies usually set 16-hour days; these long days promote vertical growth, which is important for studies that use height to measure growth. However, I wanted to promote leaf growth, not vertical growth, so I used short day lengths. Though this is not a measure of fitness, it is a measure of growth at an important life stage. Plant size is correlated with fruit production in the closely related *M. cardinalis* (Sheth and Angert 2018), and growth is likely to bear even more on fitness in species like this that regularly reproduce vegetatively.

At the beginning and end of each treatment, I photographed the trays in order to use the photographs to measure leaf area. I used a growth chamber as a temporary photo studio. I covered the light box with a light-diffusing cloth to improve photo quality and used an ad-hoc stand to ensure I took photos from directly above each tray. I used an iPhone XR to take photos. On each tray, I placed four red squares of known area that would later be used as scales to measure leaf area. See Figure 4 for an example.

Photo Processing and Leaf Area Measurements

I used Photoshop (version 22.3.0) to manually highlight and recolor all leaf area to white (R=255, G=255, B=255), all red scales to an evenly saturated red (R=255, G=0, B=0), and anything else to black (R=0, G=0, B=0). This could be done in most image editing software, but Photoshop’s “Magic Wand” tool made selecting specific areas much less tedious. I then

programmatically cropped each individual along with its closest scale. Some individuals were too large or off center to be cropped programmatically, so I cropped these individuals by hand. Ideally, I would have been able to easily insert the cropped, but otherwise unedited photos into the program Easy Leaf Area to measure leaf area (Easlon and Bloom 2014). However, the program could not accurately measure leaf area with perlite in the background. Easy Leaf Area uses three parameters related to RGB values: leaf minimum green RGB value, leaf green ratio (G/R), and leaf green ratio (G/B). Because perlite is white, it has high red, green, and blue values, and I could find no set of parameters that could discriminate between perlite and all of the leaf area for each individual. With thoughtful planting in future experiments, I expect Easy Leaf Area could be used to more easily measure leaf area, but since it was not feasible, I detail my alternate methods.

I wrote a program to determine the leaf area of each individual by comparing it to the red scale of known size. For each picture, I determined the number of pixels that represent the scale, then determined the number of pixels of leaf area, then used the known size of the scale to calculate the amount of leaf area. The program produces a copy of each image with the leaf area and scale that it measured, allowing me to verify that each individual was measured properly. This program is similar to Easy Leaf Area, however Easy Leaf Area has more sophisticated features that allow one to set minimum leaf size or if it should identify one or multiple leaf objects. Additionally, Easy Leaf Area is also quite slow, taking days to process all of my photos. Since I manually edited the photos to make analysis feasible, I wrote this program to speed up analysis. See Fig. 4 for examples of photos through this process.

Once I generated leaf area measurements, I calculated relative growth rate (RGR) as follows:

$$\frac{leafarea_{end} - leafarea_{start}}{\#_{days} * leafarea_{start}}$$

Some individuals at the temperature extremes (i.e. 5 and 40ºC) died or lost leaf area during the treatment. For these individuals, I set RGR to 0. I removed individuals whose upper leaf surface was not facing the camera, making measures of their leaf area highly inaccurate. I originally planted 2,208 individuals. 60 individuals did not germinate, and 73 were too angled to accurately measure leaf area. In total, I generated measures of RGR for 2,075 individuals.

Thermal Performance Curves

I used the *performr* (version 0.2) package to generate thermal performance curves (Tittes et al. 2019). This package includes a hierarchical Bayesian model specifically meant for building performance curves simultaneously for different biological groups (e.g. species, populations) to facilitate comparison between these groups. It has been used in several similar studies, one comparing native and invasive populations of *M. guttatus* and another with the closely related *M. cardinalis* (Querns et al. 2020; Wooliver et al. 2020). The main drawback of this model is that it does not allow for the inclusion of random effects, meaning I cannot easily evaluate if variation in RGR is from within or between seed families. Instead, I built two models, one generating a performance curve for each population and one generating a performance curve for each seed family. Though this does not allow for robust analyses of variation in RGR, it does give us some idea of the sources of variation in thermal performance traits.

For the population-level model, I first calculated the mean RGR across replicates for each seed family within each treatment. This resulted in 613 distinct RGR values. To improve model performance, I centered temperature treatment values around 0 and scaled RGR values by the overall mean of the 613 RGR values (Tittes et al. 2019; McElreath 2020). I used the default settings of the model, except that I increased the prior standard deviation for the maximum and

minimum values at which the response trait falls to zero (min_pr_sig, max_pr_sig) from 1 to 3 to increase convergence. I assessed convergence using the R-hat statistic and by visually inspecting posterior distributions and trace plots (Appendix S1 & S2). This model produced 4,000 posterior draws per population.

I performed the family-level model in a similar manner. I did not average across seed families prior to running the model, so I had 2,075 distinct RGR values. I centered temperature treatment values around 0 and scaled RGR values by the overall mean of the 2,075 RGR values. I used the same settings described above for the population-level model, except that I increased the number of iterations to 15,000 to improve convergence. This model produced 30,000 posterior draws per seed family.

I quantified model fit by calculating the Bayesian p-value, which is the probability that values drawn from the simulated posterior predictive distribution will exceed the observed values (Gelman et al. 2014; Wooliver et al. 2020). P-values closer to 0.5 indicate adequate fit between the modeled and observed data, while values at or near 0 or 1 indicate a large skew in the predictions of the model (Gelman et al. 2014). The overall Bayesian p-value for the population-level model is 0.60, while p-values for each population within the model are within the range 0.41-0.82 (Table 2) The overall Bayesian p-value for the family-level model is 0.54, while p-values for each family within the model are within the range 0.18-0.90 (Appendix S3). These values indicate that, overall, both models fit the observed data well. P-values for every population within the population-level model also indicate adequate fit. There are a handful of families within the family-level model that fit less well than would be ideal, but a large majority of p-values for each family indicate adequate fit (Appendix S3).

For both models, I first back-transformed thermal performance parameters to their original scale. I retrieved or calculated the following parameters from each draw: maximum RGR, thermal optimum, thermal tolerant breadth, and thermal performance breadth. Maximum RGR is the RGR at the peak of the performance curve. Thermal optimum is the temperature at which the maximum RGR is reached. Thermal tolerance breadth is the difference between x_max and x_min, which are the maximum and minimum values at which the response trait falls to zero. I calculated thermal performance breadth as the width of the thermal performance curve at 50% and 80% of the maximum RGR for each draw. These measures of performance breadth were always qualitatively similar so I only use breadth at 50% from here on. Performance breadth cannot be computed directly, so I calculated it from a grid of 100 equally spaced points along the temperature axis, choosing the two points that had the minimum distance to the desired percent RGR along the curve's height (Huey and Stevenson 1979; Wooliver et al. 2020). For these parameters, I calculated the 95-percentile interval and the 95% highest posterior density interval (HPDI) of the posterior draws (McElreath 2020). These two intervals always produced qualitatively similar results, so I show only the 95-percentile interval from here on. I used these intervals to compare thermal performance traits across biological groups. If the intervals for a given thermal performance parameter for two groups do not overlap, this indicates a statistically significant difference. To test the CVH, I compared the different measures of breadth (tolerance breadth, performance breadth) between coastal and inland sites to see if coastal populations have smaller breadths. I also made a quantitative comparison, by evaluating if there is a positive relationship between temperature variation at each site and niche breadth. For evidence of a specialist-generalist tradeoff, I looked for a negative relationship between breadth and maximum

RGR. Tests of specialist-generalist tradeoffs assume equal area under the performance curves (AUC), so I also checked this assumption by comparing AUC across groups.

Mechanistic Niche Model

I retrieved historical and projected climate data through the Basin Characterization Model (Flint et al. 2013). The Basin Characterization Model provides downscaled climate and hydrological data at a resolution of 270 m. I downloaded 30-year maximum and minimum temperature averages for each month of the year for two time periods: 1981-2010 and 2070-2099. For 2070-2099, I retrieved projections using two global circulation models: GFDL and PCM. For each of these models, I downloaded data for two representative concentration pathways: A2 and B1. A2 represents a "business-as-usual" emissions scenario, while B1 represents a global effort to decrease emissions. These projections cover the range of expected conditions for California (Maher et al. 2017). So, I retrieved 30-year averages of the minimum and maximum temperature for each month from these five data sets: historical 1981-2010, GFDL-A2 2070-2099, GFDL-B1 2070-2099, PCM-A2 2070-2099, PCM-B1 2070-2099.

I used the ecocrop model in the *dismo* (version 1.3-3) package (Hijmans et al. 2020). Ecocrop is a processed-based model that estimates habitat suitability based on temperature conditions. Because performance curves did not differ greatly across all populations, I made predictions for only three populations — one coastal (Pt. Reyes) and the two inland populations that differed (Mt. Diablo and Mono Lake). I estimated habitat suitability using ecocrop for each of these populations and with each of the five sets of temperature data described above. The ecocrop parameters that were unique for each population were T_{min}, T_{max}, $T_{optmin,}$ and T_{optmax}. I set T_{min} and T_{max} to the lower and upper points where performance falls to 0, respectively. For each population, I ran the model twice, once with T_{optmin} and T_{optmax} set to the lower and upper limits of the breadth of the curve at 50% the maximum RGR and once with T_{optmin} and T_{optmax} set to the limits of

breadth of the curve at 80% of the max RGR. Three parameters were the same for every population, the killing temperature (KT) and minimum (Gmin) and maximum growing (Gmax) period in days. I set KT to -100 because these populations are known to survive subzero temperatures and did not want this to influence suitability calculations. I set Gmin and Gmax both to 120 so that the growing period would calculate to 4 months, the minimum length of the growing season for any of these populations. Ecocrop can also estimate habitat suitability based on precipitation conditions, but I did not include this in the model. I also calculated where populations are projected to experience temperatures above their upper thermal limit to evaluate if temperature increases may more regularly expose populations to harmful temperature extremes.

Computation

I performed all analyses using R (version 4.0.5) and RStudio (version 1.4.1106) (R Core Team 2020; RStudio Team 2020). I created all plots using the package *ggplot2* (version 3.3.3) (Wickham 2016).

Results

Microclimate

Hourly temperature recordings from each site are highly correlated between the two loggers (.957-.999), but temperature loggers are only moderately correlated with downscaled temperature data (.663-.879). Downscaled data were generally better correlated with temperature recordings from inland sites (.778-.879) than coastal sites (.663-.769). The *microclima* and *NicheMapR* packages include methods to account for coastal climatic effects. However, the downscaled temperature data appear to slightly underestimate the temperature extremes experienced at two coastal sites (Chimney Rock and Pt. Reyes), while overestimating the variability at the other coastal site (Golden Gate). Besides this, the general distribution and

temperature extremes match between loggers and downscaled climate data (Fig. 5). Additionally, the downscaled climate summarizes well the variation in temperature experienced at most sites. From here on, I use only downscaled climate data from 1979 through 2020, though remembering the caveats discussed here.

As expected, coastal sites are generally less variable in temperature than inland sites (Fig. 5). However, all sites experience similar upper temperature extremes, though the amount of time at higher extremes is greater for more inland sites. The Mono Lake population is unique, experiencing the most variation of any population. This is not surprising given its location in the high desert just east of the Sierra Nevada, but it is interesting to note that greater variation is driven primarily by colder extreme temperatures, not hotter extreme temperatures relative to other sites.

Climatic Variability Hypothesis

I did not find support for the CVH. Coastal populations did not categorically differ from inland populations in tolerance breadth (Fig. 6) or performance breadth (Fig. 7). Even when comparing populations by their actual temperature variation, populations with greater variation did not have larger tolerance or performance breadth (Fig. 8). Populations also did not differ in the limits of their tolerance breadth (Fig. 9). Therefore, no populations differed in tolerance breadth. However, two inland populations (Mt. Diablo and Mono) differed from one another in performance breadth, with Mono having the smaller breadth (Fig. 7). This is due to Mono having a higher lower limit in its performance breadth (Fig. 10).

Family-level Model

Given that most populations did not differ in any thermal performance parameter, I unsurprisingly found much overlap in the thermal performance parameters for seed families. Interestingly, for the populations that did differ in certain parameters — Diablo and Mono in

performance breadth, maximum RGR, and thermal optimum — there is also much overlap (Fig. 11). This suggests that populations do not categorically differ in these thermal performance parameters, but instead have some individuals that share similar thermal performance curves and some that differ.

Specialist-generalist tradeoff

I found evidence of a specialist generalist tradeoff. The two populations with different performance breadth (Diablo and Mono) also have different maximum RGR in the expected direction — Diablo has a wider breadth and lower max RGR while Mono has a smaller breadth and higher RGR (Fig. 12) Across the six study populations, there is a negative correlation between mean performance breadth and mean maximum RGR (-0.863). However, there is much overlap in the percentile intervals for both parameters so this should be interpreted cautiously. Still, results from the family-level model also provide support. Across the performance curves for all seed families, there is again a negative correlation between mean performance breadth and mean maximum RGR (-0.614). The strength of this relationship varies when computing the correlation of these parameters within each population (Table 3; Fig. 13). The relationships are at least moderately negative for most populations, except Chimney Rock which is weakly negative but also had a small sample size. However, not all biological groups, in both models, have the same AUC.

Mechanistic Niche Model

Across all models, populations are projected to experience general increases in habitat suitability with increases in temperature (Fig. 14). There were small differences between model types. The global circulation models GFDL and PCM mainly differ in projections for precipitation. GFDL projects a warmer and drier climate, while PCM projects a warmer and wetter climate. Temperature projections generally differ little between these models, and

subsequent habitat suitability predictions differ even less. Similarly, the restricted concentration pathways also show minor differences. The "business-as-usual" pathway, A2, projects higher temperature increases. This leads to larger changes in habitat suitability, but differences in these changes are small in magnitude and in the same direction. There are greater differences between models that use the limits of performance breadth at 50% the maximum RGR for T_{optmin} and T_{optmax} and models that use the limits at 80% the maximum RGR. Because the model that uses breadth at 80% has a smaller ideal range of temperatures, it includes greater nuance in the changes of habitat suitability. Again, these changes are in the same direction and differences are small in magnitude. For these reasons, I show only projections from the GFDL-A2 model with T_{optmin} and T_{optmax} set as the limits of performance breadth at 80% the maximum RGR to highlight general patterns in changes of habitat suitability.

Populations generally experience increases in habitat suitability, both when comparing the amount of suitable habitat state-wide map and when comparing the value of suitability in their current location (Fig. 14 & Fig 15). Projections between populations show some differences on the state-wide map, but since these projections are based only on mean values of thermal performance curves that are very similar, I do not want to emphasize small differences in habitat suitability between populations. Notably, at a regional scale, all populations experience increases in habitat suitability while still avoiding temperature extremes above their upper tolerance limit (Fig. 16).

Discussion

CVH

Unexpectedly, I found no support for the CVH. Coastal populations did not differ in thermal niche breadth from inland populations, and there was not a positive relationship between niche breadth and temperature variation at each site. Even more surprisingly, the population that

experiences the greatest temperature variation, Mono, actually had the smallest mean niche breadth and only differed in this thermal niche trait from another inland population. Previous studies of the CVH using plants have given mixed support (Sentinella et al. 2020; Wooliver et al. 2020). The lack of differentiation in performance curves is congruent with a recent study comparing native and invasive populations of *M. guttatus* (Querns et al. 2020). Querns et al. found no evolution of thermal performance parameters in the invasive range and no adaptive clines in thermal performance breadth with latitude or temperature seasonality. They concluded that broad thermal tolerance rather than adaptation to new thermal conditions has promoted the invasiveness of this group (Querns et al. 2020). Interestingly, it is thought that invasive populations are derived from the coastal ecotype, so they included only coastal populations in their study. Given that coastal populations of *M. guttatus* have unique adaptations to their coastal environment (Lowry et al. 2019*a*; Popovic and Lowry 2020), we must wonder why they have not differentiated in thermal performance traits.

Figure 17 shows the relationship between each population's thermal performance curve and historical temperature. This figure reveals three important details. (1) Two coastal populations (Chimney Rock and Pt Reyes) only experience a small range of temperature relative to what they can handle. (2) One coastal population (Golden Gate) deals with a range of temperatures similar to inland populations. (3) Mono Lake is not equipped to grow under the large amount of cold it regularly experiences. Though these details cannot fully explain why this system does not conform to the CVH, they shed some light on thermal niche evolution in this group and provide directions for further research.

If we were to observe only Chimney Rock and Pt. Reyes in Figure 17, we may conclude that coastal populations are maintaining wider thermal performance curves than expected.

However, Golden Gate more regularly experiences a greater range in temperature, despite being a coastal site. Additionally, these coastal sites likely experience higher temperature extremes than shown here, according to the mismatch between the downscaled and *in situ* temperature data (Fig. 5). Coastal sites may not be as stable as we assumed, and certainly some coastal areas are more variable than others. Gene flow between variable and stable coastal microclimates may maintain wide thermal performance curves across all populations and be essential for the long-term persistence of this group. Interestingly, the inland population closest to the coast, Mt. Burdell, did not differ in any thermal performance parameter compared to coastal populations. Effectively, this population and the coastal ones all have the same thermal performance curves, while the two other inland populations differ slightly. When considering the role of gene flow in maintaining wide thermal performance curves on the coast, it may be important to consider inland populations as well. One must move only a few kilometers inland to see much greater fluctuations in temperature (Fig. 2) and high rates of gene flow have been shown between coastal and inland ecotypes (Twyford et al. 2020). Temperature extremes are known to impose strong selection on thermal performance (Kingsolver and Watt 1983), and low levels of gene flow can easily spread favorable alleles (Rieseberg and Burke 2001; Morjan and Rieseberg 2004). In other words, if selection imposed by temperature extremes is strong enough, even a small amount of gene flow between thermally stable and thermally variable sites may maintain wider thermal performance curves across all populations. This may be an area that is deserving of further research.

The Mono Lake population has perhaps the most distinct performance curve, which is not surprising given that it is the most distant population, but these differences are not in the expected direction. Mono experiences similar upper temperature extremes as other populations

(Fig. 5) so its increase in temperature variation is due to the lower temperature extremes it experiences over winter. However, Mono does not perform better at colder temperatures than other populations. In fact, Mono may actually perform worse. All populations share the same lower limit of the tolerance breadth (Fig. 9). However, Mono has a significantly higher lower limit of its performance breadth (Fig. 10) and a higher temperature optimum than most other populations (Fig. 18). Here, it is very important to remember that these traits are relative to growth in leaf area. Across plants, cold tolerance is relatively labile both within and between species, with many plants able to tolerate temperatures well below freezing (Araújo et al. 2013). This perennial population at Mono Lake survives through very cold temperatures that other populations never experience, but its leaf growth is greatest at a smaller range of warmer conditions. Perhaps this should not be surprising, as this population likely has the shortest growing season and must take advantage of warmer conditions when they are present, while coastal populations can grow year-round. It is interesting to note here that Mono Lake also has the highest maximum RGR, though this only significantly differs from a few other populations (Fig. 19).

Thermal Tolerance and Thermal Performance

In this study I explicitly compared thermal tolerance breadth and thermal performance breadth. In both the population-level model and family-level model, I found no differences in the overall tolerance breadth or the upper and lower limits of tolerance breadth across all biological groups (Fig. 6 & 9). Though cold tolerances can be labile within species (Araújo et al. 2013), the range of temperatures under which leaf growth can occur is conserved across all groups in this study. However, in both models, I found some differences in the overall performance breadth and performance breadth limits (Fig. 7 & 10). In other words, these populations have evolved different performance breadths but have not evolved different tolerance breadths. It is interesting

to again consider Figure 17 here and notice that no population has its optimum at the most common temperature, but no population regularly experiences temperatures above the upper limit of their performance curve.

Temperature extremes can impose strong selection (Kingsolver and Watt 1983), but if relevant traits are constrained in some way, temperature extremes can also set the boundary of where organisms can exist (Overgaard et al. 2014). If the thermal tolerance of an organism is constrained, then we may expect evolution to occur in the thermal performance. Theoretical work has shown that organisms can tolerate a broad range of conditions while specializing their performance on a relatively small range of conditions (Gilchrist 1995). I know of no empirical work on this topic, which has implications for the evolution of organisms under climate change. If performance breadth proves to be a more labile trait, evolution in performance breadth may buffer organisms against climatic changes. However, as we experience greater climatic extremes, constraints on the evolution of tolerances may make evolution in performance breadth irrelevant. Further research is needed, and this species, with similar tolerances but different performance, could prove a useful study system.

Specialist-Generalist Tradeoff

I found evidence for a specialist-generalist tradeoff both between and within populations (Fig. 12 & 13). However, AUC was different for groups within both models as well, meaning the assumption that AUC is constant was not met. These results are again in agreement with the study of native and invasive populations of *M. guttatus* (Querns et al. 2020). As in that study, there is a strong positive correlation between AUC and max RGR, while there is not a strong correlation between AUC and performance breadth (Table 4). This suggests that there is not a simple trade-off between peak performance and breadth. Instead, increases in peak performance can reduce performance breadth while increasing the overall thermal niche space (Querns et al.

2020). The physiological basis for the expectation of a simple tradeoff is the increased energetic cost of maintaining performance over a wide range of conditions (Somero 1995). However, physiological responses to changes in a certain condition can be complex, such that tradeoffs in performance can be avoided (Angilletta et al. 2003). Though there is evidence of a simple specialist-generalist tradeoff in the closely-related *M. cardinalis* (Angert et al. 2011), these results join a large body of empirical work that does not support a simple specialist-generalist tradeoff (Angilletta 2009).

Mechanistic Niche Model

All populations generally show increases in habitat suitability with projected temperature increases (Fig. 14). Across the state of California, declines are only projected for areas that currently reach extreme warm temperatures, like the Central Valley and southeastern deserts. Temperature increases in these areas drive conditions above suitable temperatures, but these decreases are minor. However, if we focus on suitability in the regions around the locations of these populations, we only see increases in suitability (Fig. 15). As seen in Figure 17, the most common historical temperatures are below the optima for every population. Therefore, increases in temperature lead to greater suitability as temperatures move closer to the optima. Given that populations currently rarely experience temperatures above their upper tolerance limit (Fig. 17), I evaluated if temperature increases might expose plants to more harmful temperature extremes. This appears to not be the case, as no population is projected to experience more extremes beyond their limit within the region they currently occupy (Fig. 16). When solely considering the thermal niche of these organisms, it appears climate change may improve the conditions for these populations at no cost. However, this model does not consider changes in precipitation and water availability.

During the thermal performance experiment, I provided plants with plentiful water, mimicking the seeps and streams these plants usually grow in. However, climate change may bring decreases in precipitation (Flint et al. 2013). Increases in temperature are also leading to greater aridity across North America (Overpeck and Udall 2020). Additionally, coastal populations are expected to lose fog cover, leading to even warmer, drier habitat (Kawai et al. 2018). These changes in water availability may decrease the amount of suitable habitat and the duration that habitat is available. Temperature increases may allow plants to grow faster and buffer against this loss in water availability, but it may also compound the threat. In a hydrothermal evaluation of performance on three frog species, researchers found performance declined rapidly when lower hydration was combined with higher temperatures (Greenberg and Palen 2021). More research is needed to confirm how *M. guttatus* performs under different hydrothermal conditions.

Originally, I hoped this mechanistic model could be used to forecast how populations may respond differently to climate change. However, since thermal performance curves did not differ much, suitability forecasts did not differ much (Fig. 14). Additionally, the model only uses population mean thermal performance traits, so any differences may not be very meaningful. A large improvement could be made on these predictions by taking advantage of the Bayesian nature of the thermal performance curve model to estimate uncertainty around habitat suitability predictions. Instead of using population averages, one could perform *ecocrop* using parameters from each posterior draw, then describe suitability for each population as a percentile interval. Especially with performance curves that have small differences, like the ones in this study, this method would better show similarities in suitability predictions and properly

incorporate uncertainty in our estimations. However, this is extremely computationally intensive and was not feasible for this project.

Caveats and Limitations

Though this study does not support the CVH, it is certainly not a refutation of it, even for coastal systems. I used coastal and inland populations of a widespread species, but coastal lineages that have been more isolated from inland lineages may show greater specialization in their thermal niche. Additionally, future studies should carefully consider favorable conditions for their measure of performance, and if variation in that condition should lead to variation in performance. For example, I measured leaf growth, a trait that is heavily dependent on photosynthesis, which in turn is dependent upon temperature (Falk et al. 1996). Though the populations I studied inhabit remarkably different climates, leaf growth may be relatively constrained to a range of temperatures that are favorable for photosynthesis. Even a study using *M. guttatus* may provide greater support for the CVH if researchers are able to more explicitly test survival at colder temperatures.

I measured growth for one week at an early life stage. Though this surely bears on future fitness, it is not a measure of fitness. The thermal niche of an organism can vary across its life (Donohue et al. 2010; Müller et al. 2018), and changes in temperatures will have effects on other plant functions, notably phenology (Gremer et al. 2019, 2020). A more comprehensive study of the fitness of *M. guttatus* across a range of temperatures may reveal different patterns in thermal performance traits. More comprehensive studies would also allow for more accurate predictions of future habitat suitability. The model I presented only produced suitability evaluations for thermal conditions during this early life stage. Though this is informative, it is simplistic. To generate forecasts that could be useful to conservationists and land managers, more detailed

consideration of the environmental niche of a species are necessary. Lastly, the predictions also assume populations will not evolve new thermal performance traits. Though *M. guttatus* shows little adaptation to different thermal habitats (Querns et al. 2020) and a 7-year resurrection study with the closely related *M. cardinalis* revealed little evolution to changing thermal conditions (Wooliver et al. 2020), this assumption may still be invalid. Climate change is imposing greater temperature changes and we are predicting over much longer time scales. Climate change is also bringing about greater temperature extremes (Seneviratne et al. 2014), which may impose especially strong selection (Kingsolver and Watt 1983). Predictions that incorporate adaptive capacity often project decreased vulnerability (Bush et al. 2016). More work is needed to fully understand how *M. guttatus* will respond to temperature increases.

Conclusion

In this project, I performed a thermal performance experiment with coastal and inland populations of *Mimulus guttatus*. I used results from this experiment to test the Climatic Variability Hypothesis and evaluate how climate change may change habitat suitability for these populations. Though I found no support for the CVH and little differentiation between the thermal performance curves of coastal and inland populations, avenues for future research have arisen. First, though coastal populations are adapted to their unique environments (Lowry et al. 2019*a*; Popovic and Lowry 2020), they are not specialized on the stable temperatures that usually occur along the coast. Though we have seen that some coastal areas can experience greater temperature fluctuations (Fig. 5), more research is necessary to confirm if this has influenced thermal niche evolution in these populations. Second, other research has shown that *M. guttatus* defies expectations of its thermal niche evolution, maintaining wider thermal niches across a range of thermal regimes (Querns et al. 2020). Though this test of the CVH with *M. guttatus* did not provide support, this species may be the exception instead of the rule. More tests

of the CVH using coastal and inland organisms are necessary to better understand if the CVH has any bearing on thermal niche evolution along the coast. Third and last, climate change is projected to bring more favorable temperatures for all of these populations, but only if these populations have plentiful water. More research is needed to understand how *M. guttatus* will perform under warmer temperatures and drier conditions. I expect that for species like *M. guttatus* that are dependent on high levels of water availability, the negative impacts from drier conditions will outweigh any benefit from warmer, more favorable temperatures.

Tables

Table 1. Information on population location, maternal families collected, and full-sibling families produced in control crosses.

Population	Latitude	Longitude	Collected	Produced
Chimney Rock	37.99393	-122.9737	10	8
Mt. Diablo	37.86740	-121.9446	14	14
Golden Gate	37.82957	-122.4846	12	12
Mono Lake	38.01786	-119.1288	20	14
Mt. Burdell	38.13510	-122.5795	15	14
Pt. Reyes	38.07464	-122.9759	20	15

Table 2. Bayesian p-value for each population in the population-level thermal performance curve model.

Population	p-value
Chimney Rock	0.46425
Pt. Reyes	0.64575
Golden Gate	0.41200
Mt. Burdell	0.75975
Mt. Diablo	0.48850
Mono Lake	0.82225

Table 3. Pearson correlation coefficient between performance breadth and maximum RGR among seed families within each population.

Population	Correlation Coefficient
Chimney Rock	-0.1825084
Pt. Reyes	-0.6610300
Golden Gate	-0.5548420
Mt. Burdell	-0.5814412
Mt. Diablo	-0.3773967
Mono Lake	-0.6519668

Table 4. Pearson correlation coefficient between AUC and either maximum RGR or performance breadth.

Group	AUC-Max RGR Correlation Coefficient	AUC-Breadth Correlation Coefficient
Chimney Rock	0.8557699	0.35172078
Pt. Reyes	0.9616827	-0.43131935
Golden Gate	0.8456038	-0.02664510
Mt. Burdell	0.8446630	-0.06031578
Mt. Diablo	0.9703109	-0.14327892
Mono Lake	0.9712304	-0.45435855
Across Populations	0.9501522	-0.66455763
Across Families	0.9247440	-0.27184392

Figures

Figure 1. Schematic of performance curve with labels for the tolerance breadth and performance breadth

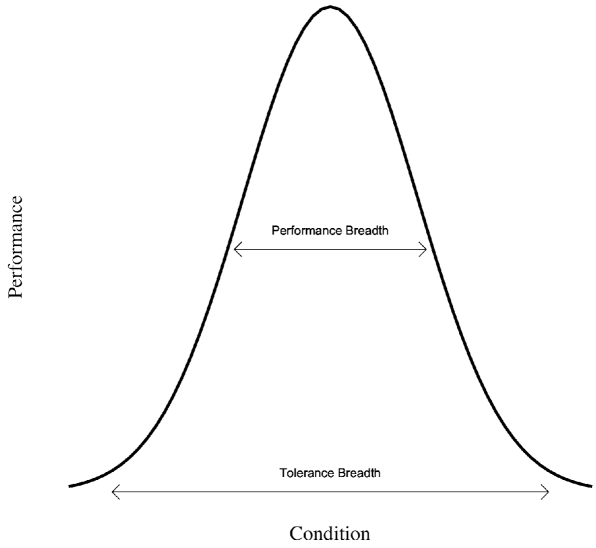


Figure 2. Mean maximum (red) and minimum (blue) temperature with standard deviation for each month over the last 40 years. Sites include 3 populations of *M. guttatus*, one coastal and two inland, and one tropical site, Panama City, for comparison.

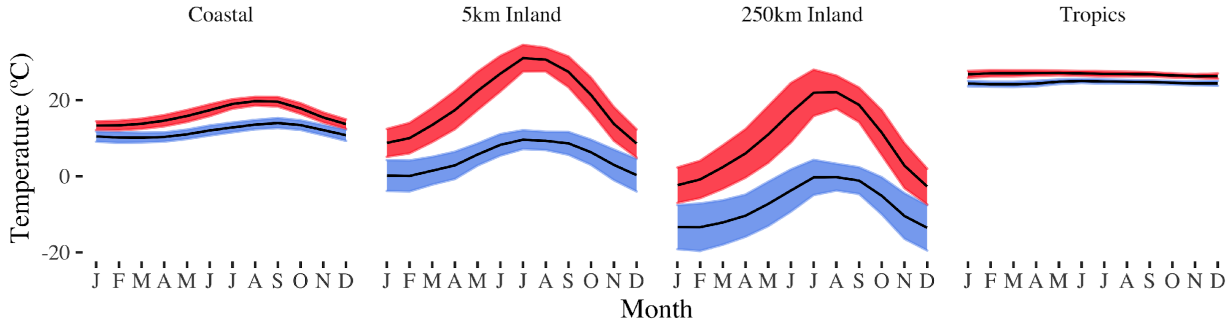


Figure 3. Map of populations.

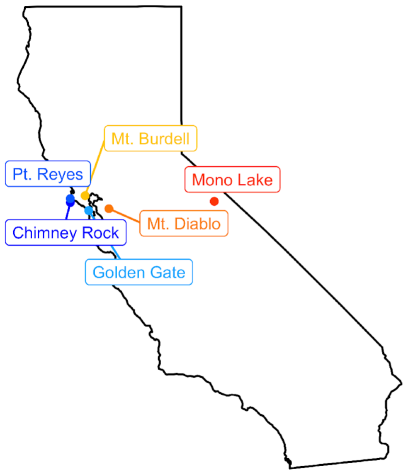


Figure 4. Images from photo processing during performance experiment. (A) Unedited photo of tray. (B) Photo of tray with leaf area highlighted as white, scale highlighted as red, and background colored black. (C) An individual plant cropped with its closest scale. (D) The output from the program that measures leaf area, indicating that the full leaf area and scale were recognized.

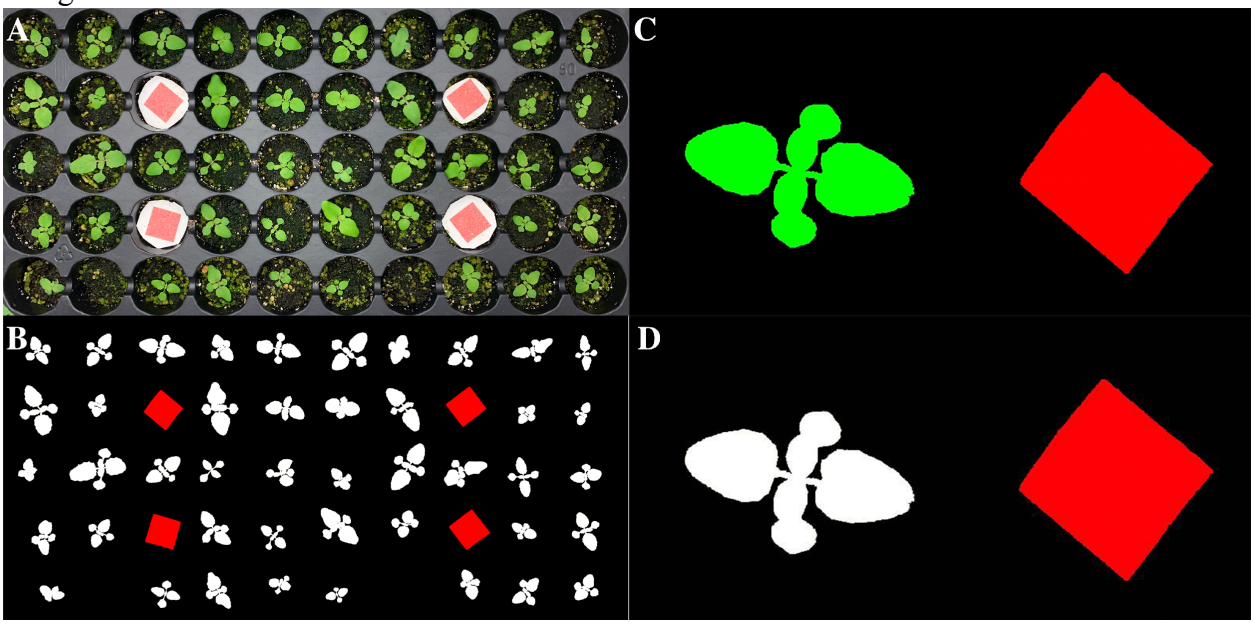


Figure 5. Temperature data from downscaled climate data and HOBO temperature loggers. (A) Violin plot of hourly temperature from each temperature logger and the downscaled climate data between the time loggers were in the field (September 2019 - January 2021). (B) Variation in temperature, measured as the standard deviation of all hourly temperature measurements across the same time period from each data source for each site.

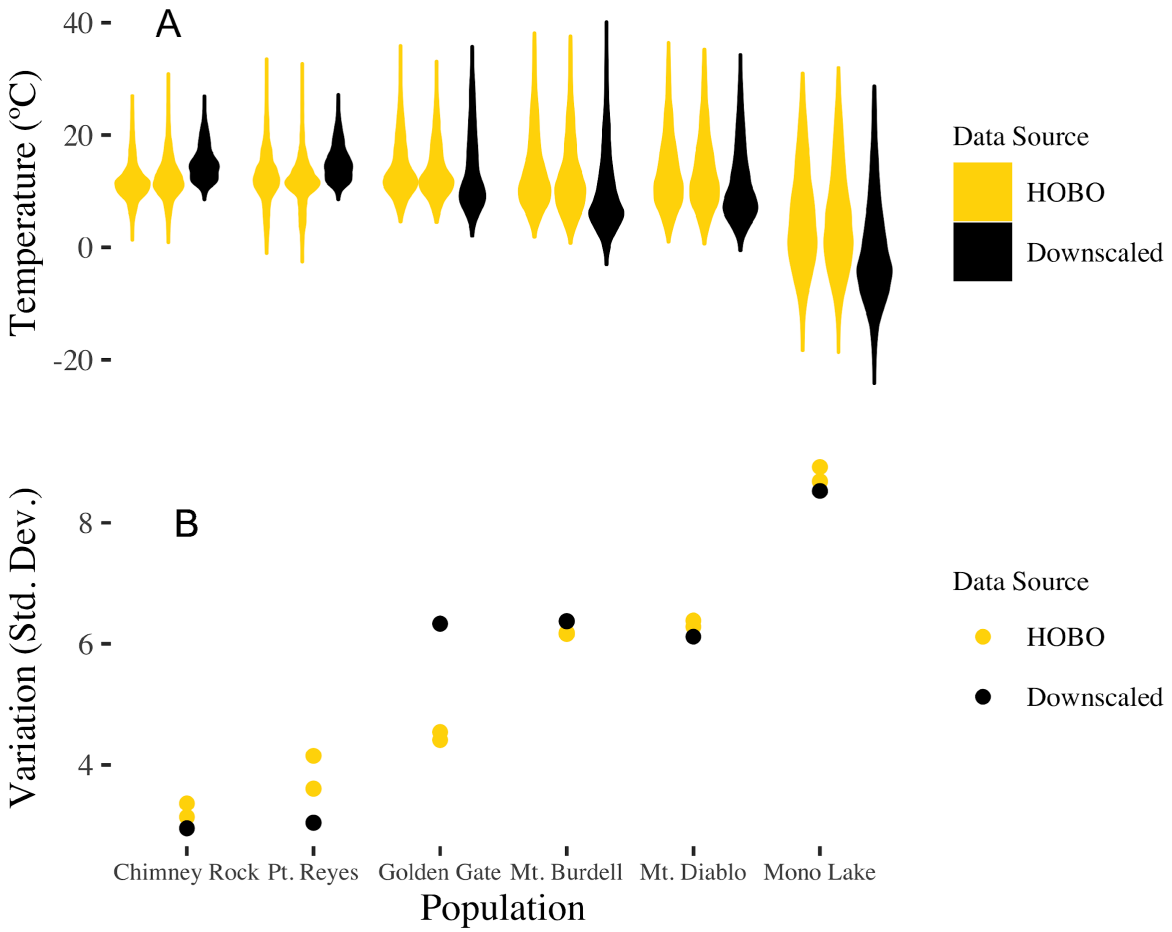


Figure 6. 95-percentile interval for tolerance breadth for each population. No populations differ in tolerance breadth.

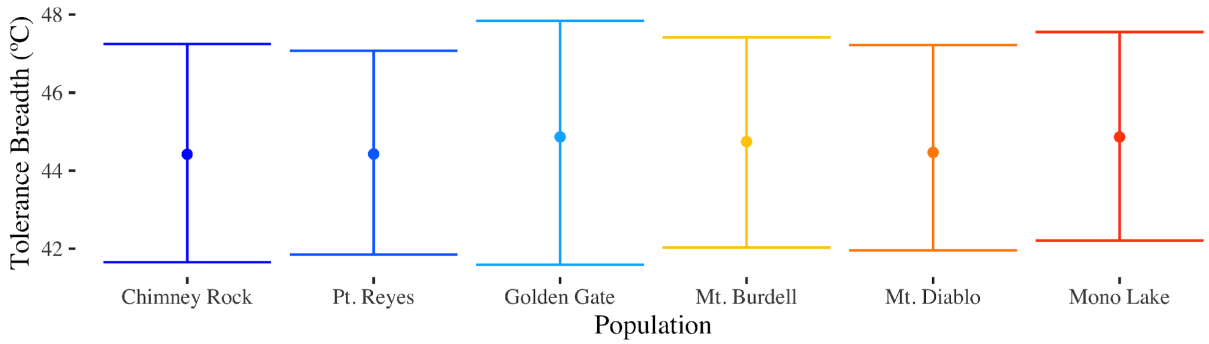


Figure 7. 95-percentile interval for performance breadth for each population. No coastal population is significantly different than an inland population in performance breadth. Only two inland populations, Mt. Diablo and Mono Lake, differ significantly in this trait.

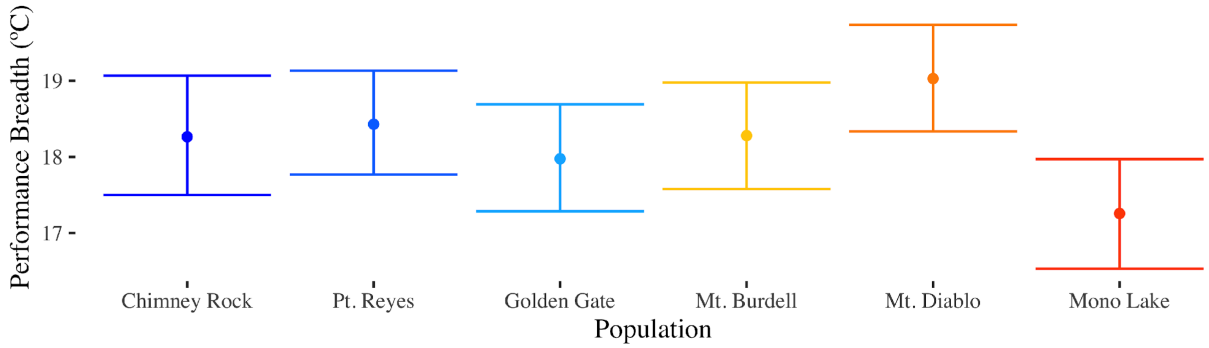


Figure 8. 95-percentile interval for performance breadth against temperature variation at each site. There is no relationship between performance breadth and temperature variation.

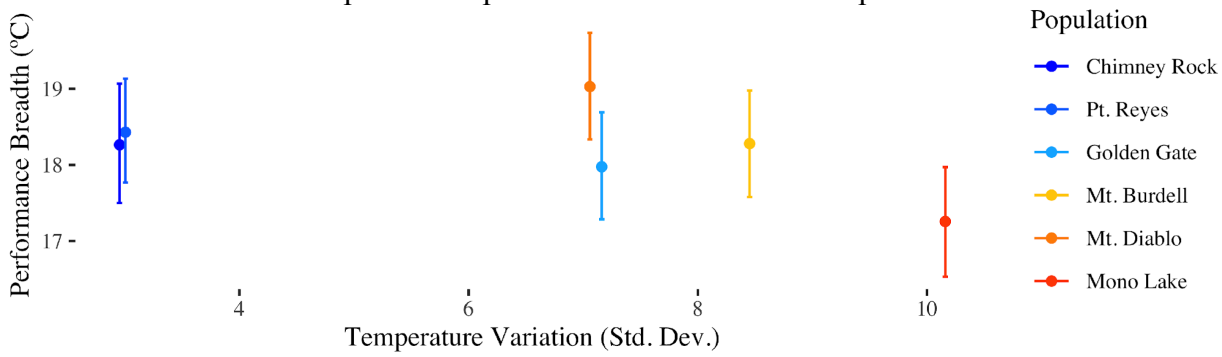


Figure 9. 95-percentile interval for lower and upper limits of tolerance breadth for each population. No populations differ in either the upper or lower limits in their tolerance breadth.

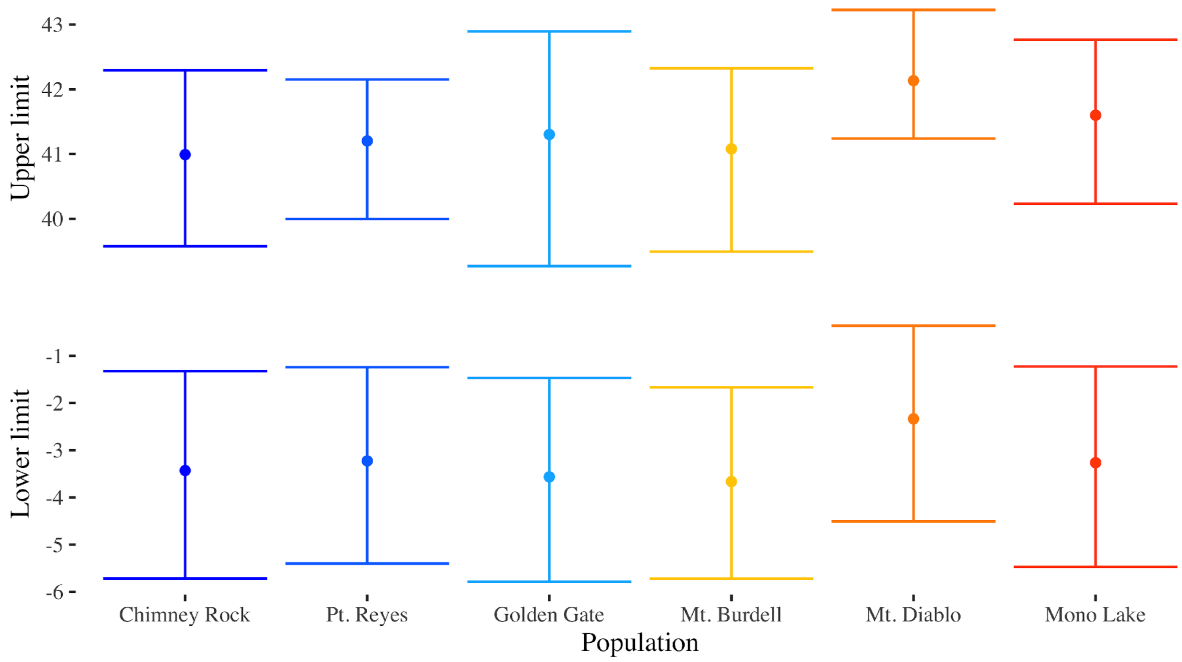


Figure 10. 95-percentile interval for lower and upper limits of performance breadth for each population. No populations differ in the upper limit of their performance breadth, but Mono Lake has a significantly higher lower limit than any other population. This difference underlies Mono Lake smaller performance breadth.

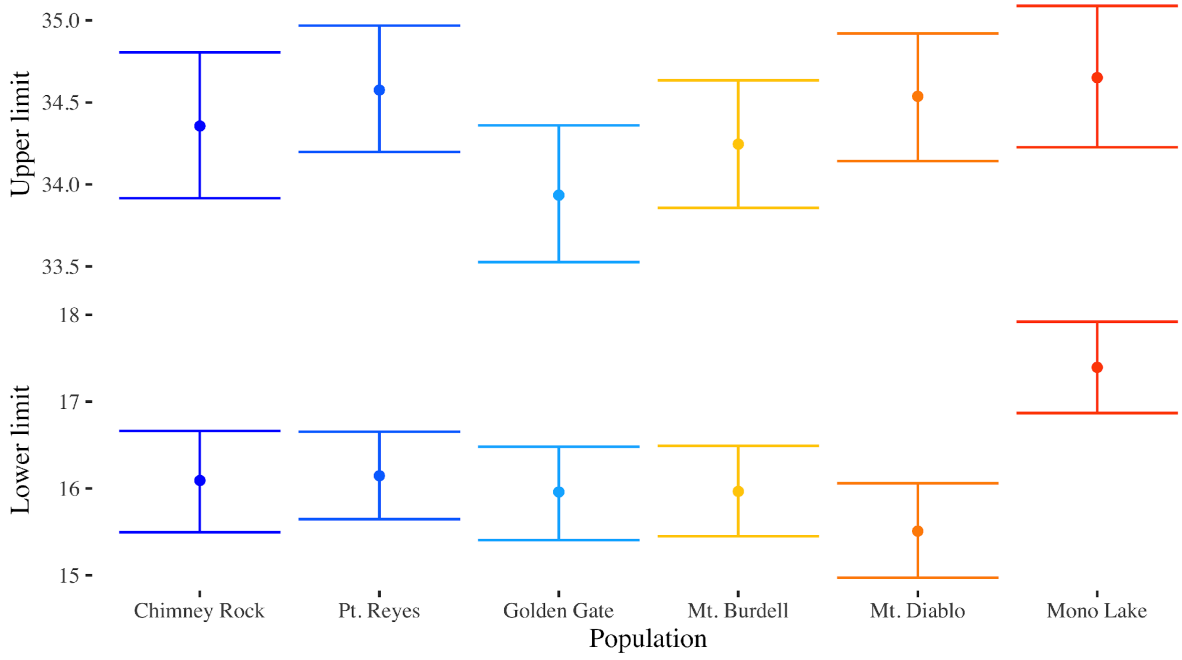


Figure 11. 95-percentile intervals for performance breadth, max RGR, and optimum temperature for each seed family from the family-level model. There is overlap between families across all populations, even those with significant differences in these traits in the population-level model. This suggests that populations do not completely differ in these traits, while having some families that overlap and some that do not. It is important to note that the families within each population are not ordered the same way across the three plots, such that the three points along the same vertical line do not represent the same seed family. I ordered families from smallest to largest for the given trait in order to facilitate comparisons between populations.

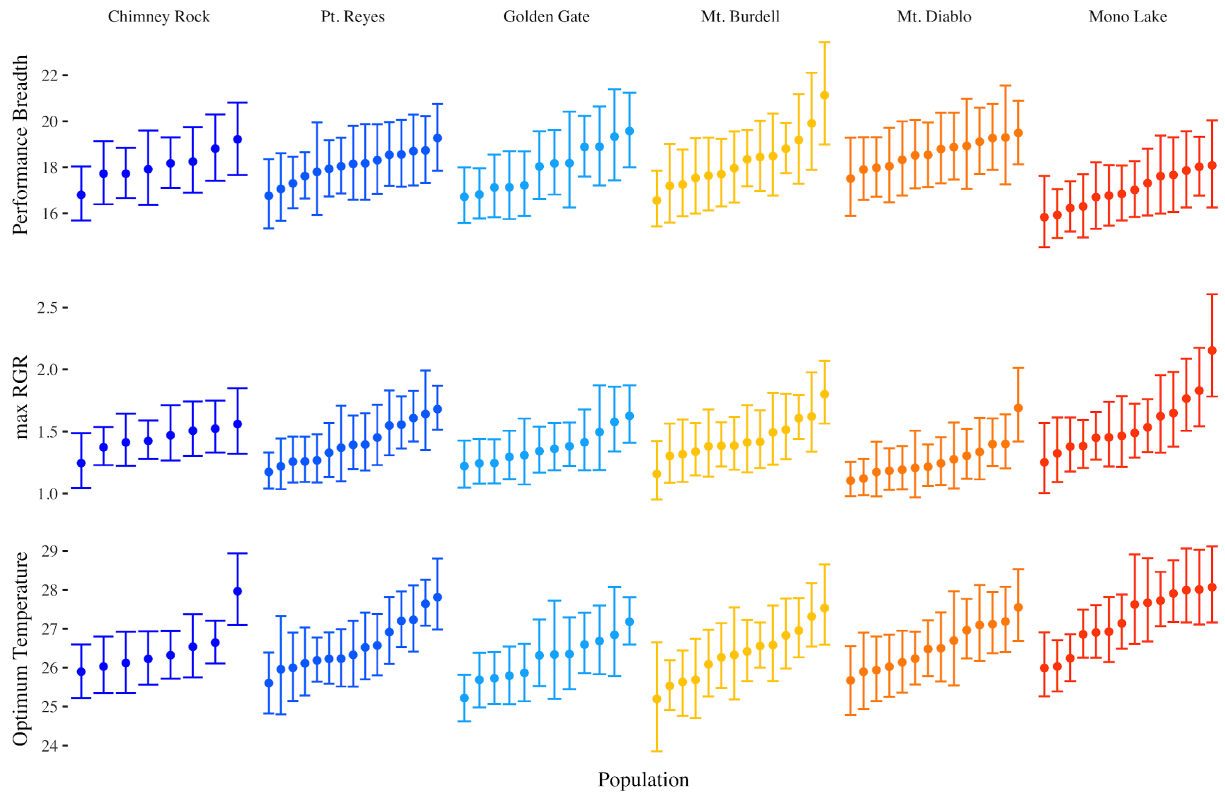


Figure 12. Max RGR against performance breadth for each population, with 95-percentile interval for both. There is a negative correlation, suggesting a tradeoff between max RGR and performance breadth. The Pearson correlation coefficient is -0.863.

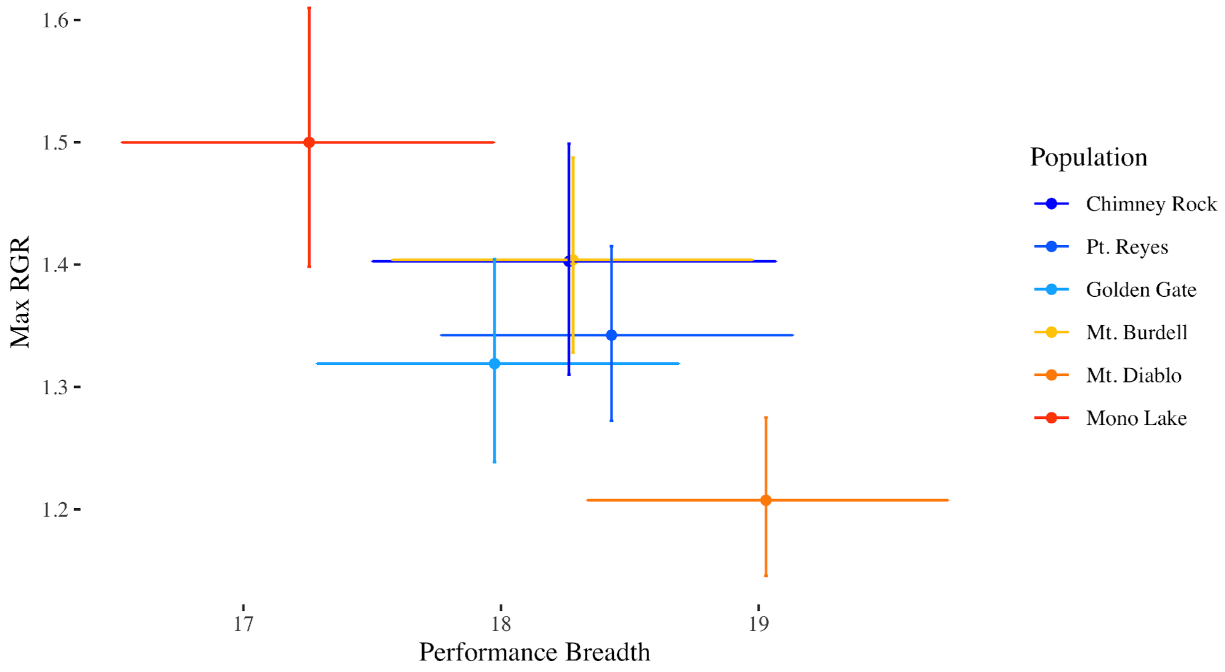


Figure 13. Mean max RGR against mean performance breadth for each seed family from family-level model. (A) All seed families together; (B) Each population plotted separately. All populations have a negative correlation between max RGR and performance breadth, suggesting a tradeoff between the two. See Table 3 for Pearson correlation coefficients.

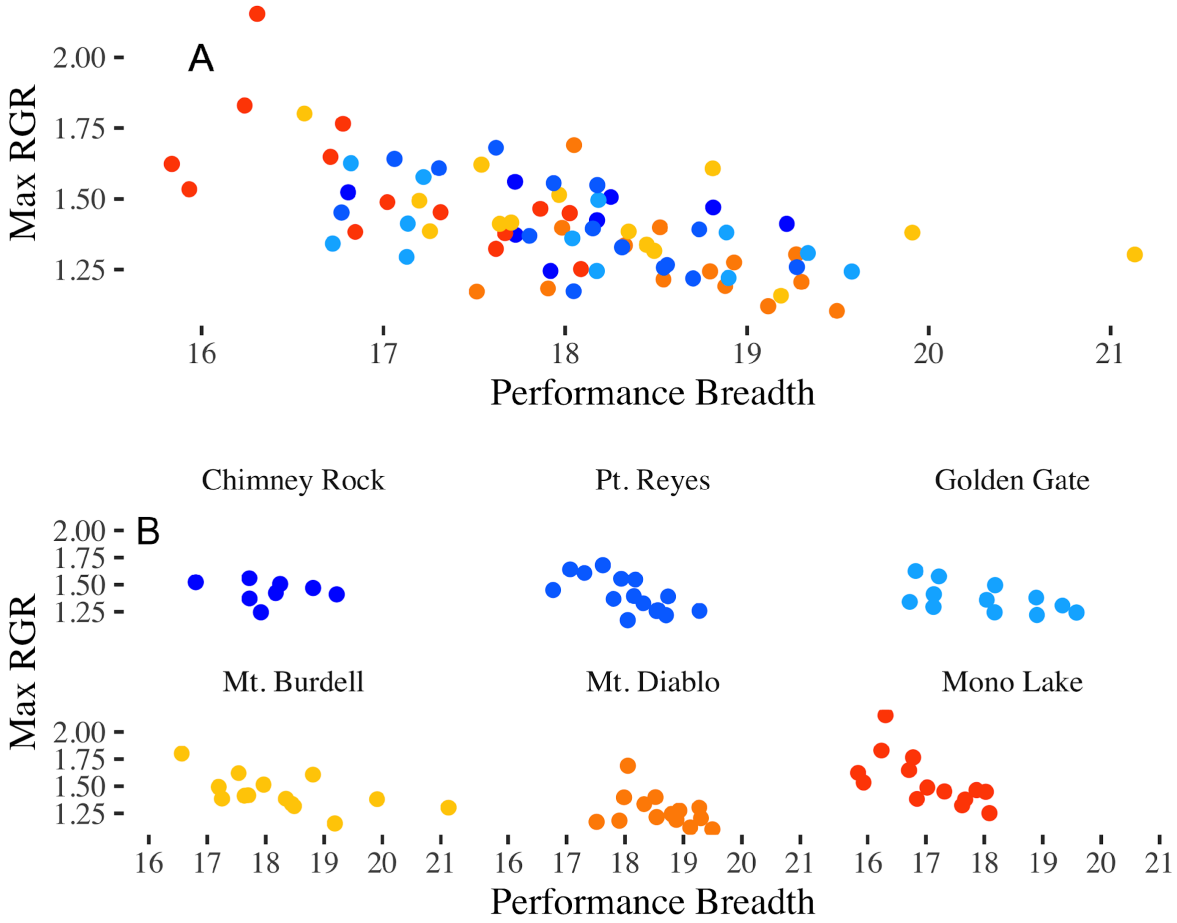


Figure 14. State-wide map of differences between habitat suitability from historical data and GFDL-A2 projection. Overall populations experience increases in habitat suitability across the state except for areas that are already the warmest parts of the state, the southeastern deserts and southern Central Valley.

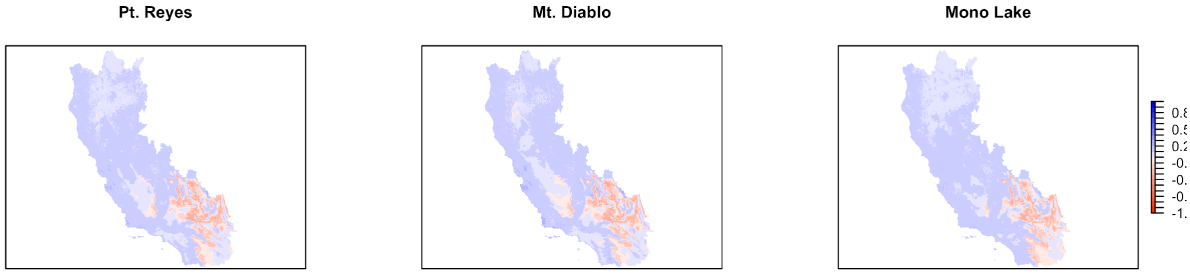


Figure 15. Regional map of differences between habitat suitability from historical data and GFDL-A2 projection. The black point represents the location of the population; each map covers about a 12000 km^2 area. All populations experience only increases in habitat suitability in their current region.

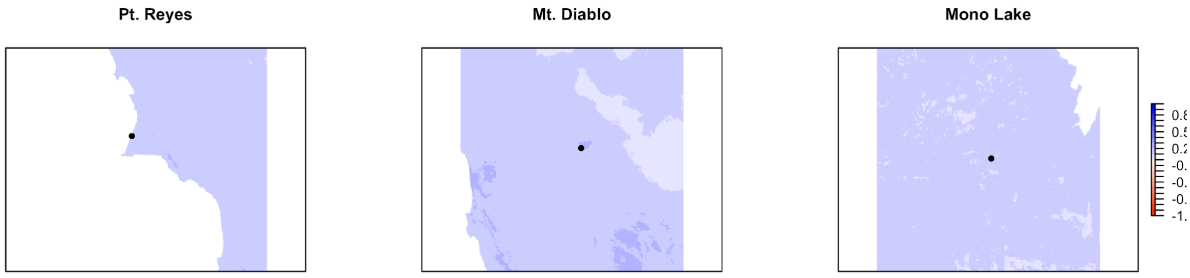


Figure 16. Statewide map showing areas in red that are projected to experience temperature extremes above the upper tolerance limit for each population under the GFDL-A2 model. Notably, none of these areas fall in the regions around the populations.

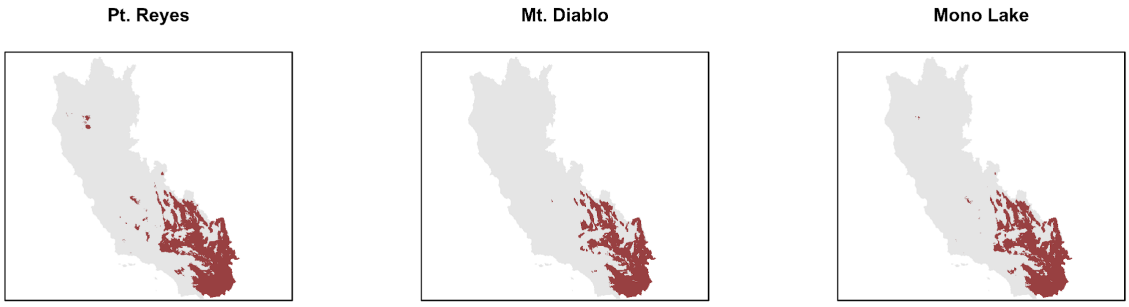


Figure 17. Temperature density plot for each site with thermal performance curve for each population. Grey distributions represent temperature density and colored lines represent thermal performance curves. Chimney Rock and Pt. Reyes only experience a small range of temperatures relative to the width of their performance curves, while the other coastal population, Golden Gate, experiences a range of temperatures that match the width of its curve and is more similar to the inland populations. Mono Lake regularly experiences cold temperature that it cannot grow under. Notably, no population's thermal optimum is at the most regularly experienced temperature.

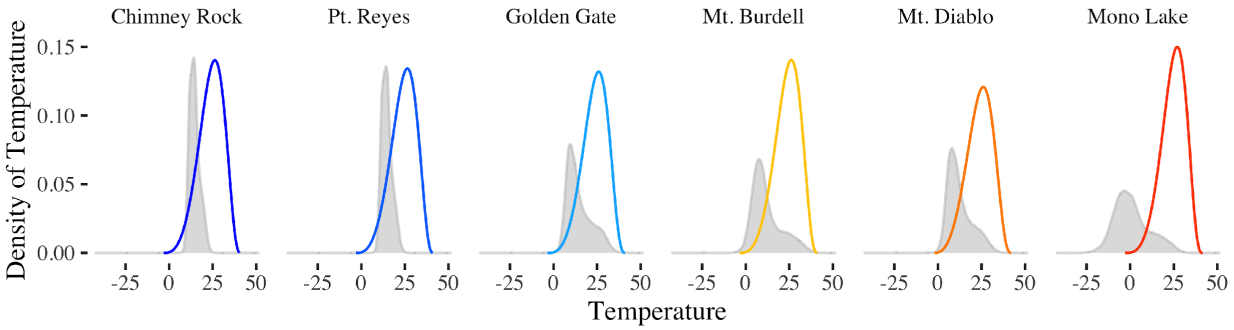


Figure 18. 95-percentile interval for optimum temperature for each population. Mono Lake has a significantly higher thermal optimum than the two other inland populations and one coastal population.

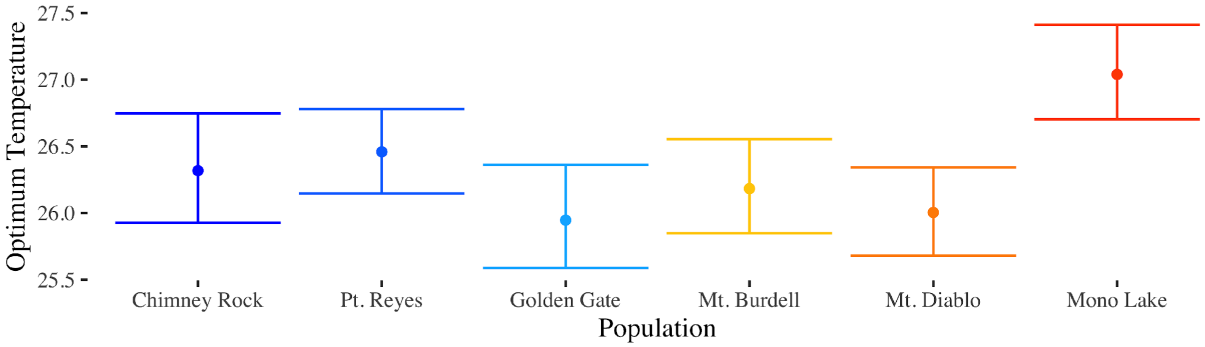
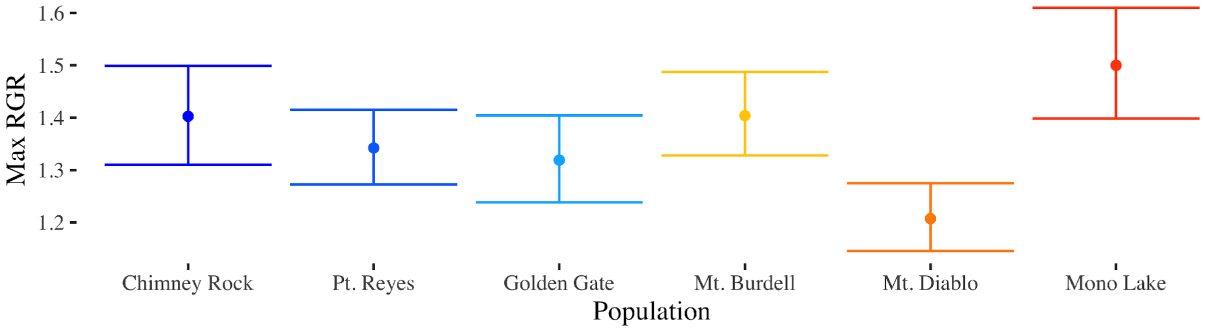


Figure 19. 95-percentile interval for max RGR for each population. No coastal population differs from an inland population, but Mt. Burdell and Mono Lake have significantly higher max RGR than the other inland population, Mt. Diablo.



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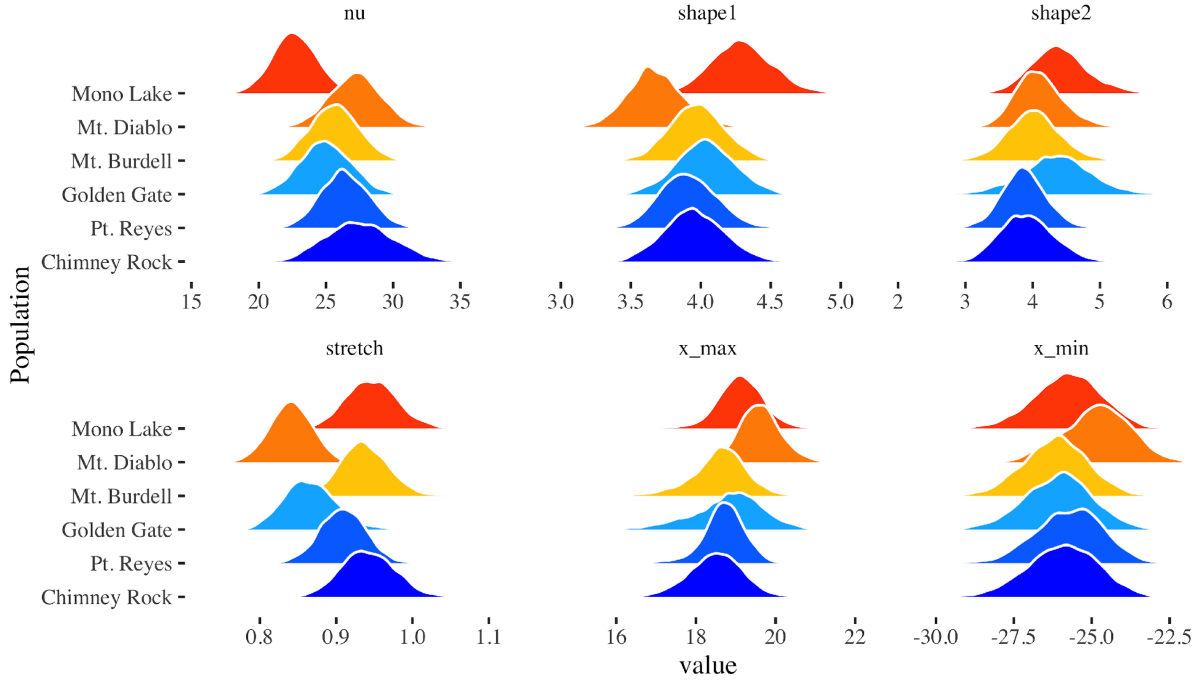
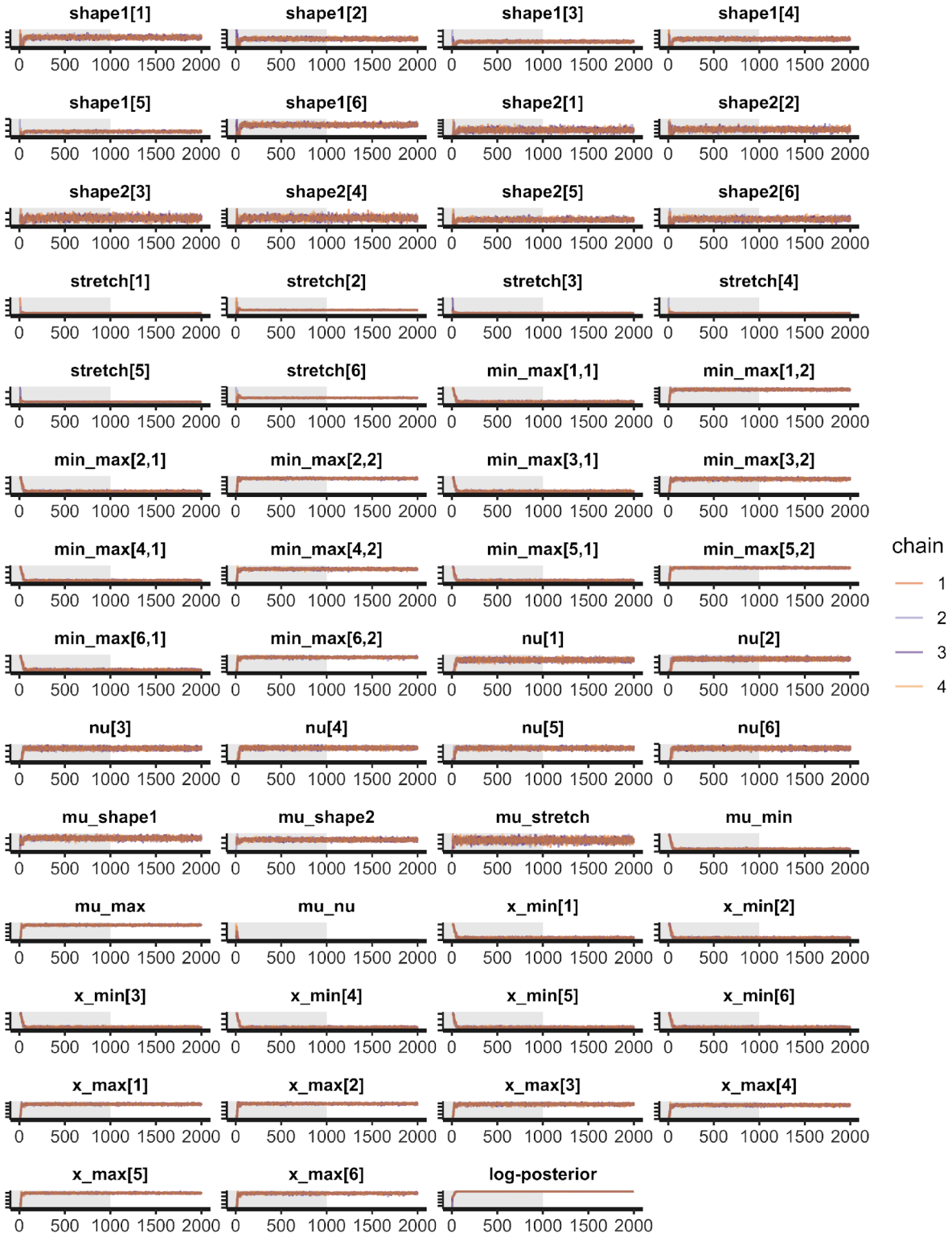
Appendix

S1. Posterior distributions from the population-level *performr* model. Definitions of parameters provided from Tittes. et al 2019. Nu: variance parameter. Shape1: First of the two parameters that modifies curve asymmetry; when shape1 is larger than shape2, the curve will skew right. Shape 2: Second parameter that modifies curve asymmetry; when shape2 is larger than shape1, the curve will skew left. Stretch: Dictates the maximum expected value of the response trait. X_max: Location along the environmental axis right of the optimum where the response trait falls to 0. X_min: Location along the environmental axis left of the optimum where the response trait falls to 0.



S2. Trace plots from the population-level *performr* model. Gray background shading represents the warmup period.



S3. Table of Bayesian p-values for each seed family in the family-level thermal performance curve model.

Population	Family	p-value
Chimney Rock	1	0.3840333
Chimney Rock	2	0.4652000
Chimney Rock	3	0.7852333
Chimney Rock	4	0.5877000
Chimney Rock	6	0.5419000
Chimney Rock	7	0.4344333
Chimney Rock	9	0.4887667
Chimney Rock	10	0.4708000
Pt. Reyes	3	0.8836667
Pt. Reyes	5	0.3868667
Pt. Reyes	7	0.8896000
Pt. Reyes	8	0.4779000
Pt. Reyes	9	0.8102333
Pt. Reyes	10	0.4334667
Pt. Reyes	11	0.4135333
Pt. Reyes	12	0.4137333
Pt. Reyes	13	0.3185333
Pt. Reyes	14	0.2083333
Pt. Reyes	15	0.3883000

Pt. Reyes	16	0.3894000
Pt. Reyes	17	0.5382333
Pt. Reyes	19	0.7645000
Pt. Reyes	20	0.3126333
Golden Gate	1	0.8039000
Golden Gate	2	0.2189333
Golden Gate	3	0.5135667
Golden Gate	4	0.7444000
Golden Gate	5	0.6942333
Golden Gate	6	0.2146000
Golden Gate	7	0.2542333
Golden Gate	8	0.6119000
Golden Gate	9	0.4018000
Golden Gate	10	0.5388667
Golden Gate	11	0.6971333
Golden Gate	12	0.6895667
Mt. Burdell	1	0.1751333
Mt. Burdell	2	0.7493000
Mt. Burdell	3	0.4540333
Mt. Burdell	4	0.2626667
Mt. Burdell	5	0.4475333
Mt. Burdell	6	0.3996000

Mt. Burdell	8	0.2034667
Mt. Burdell	9	0.7061333
Mt. Burdell	10	0.8642333
Mt. Burdell	11	0.5567667
Mt. Burdell	12	0.7705667
Mt. Burdell	13	0.5328333
Mt. Burdell	14	0.4967667
Mt. Burdell	15	0.4125333
Mt. Diablo	6	0.5334333
Mt. Diablo	7	0.5611667
Mt. Diablo	8	0.7009333
Mt. Diablo	9	0.6769667
Mt. Diablo	10	0.7789333
Mt. Diablo	11	0.2122333
Mt. Diablo	12	0.6831333
Mt. Diablo	13	0.8625000
Mt. Diablo	14	0.5448333
Mt. Diablo	15	0.4202333
Mt. Diablo	16	0.7322000
Mt. Diablo	17	0.3912333
Mt. Diablo	18	0.5172667
Mt. Diablo	19	0.6328000

Mono Lake	1	0.5180000
Mono Lake	3	0.4755667
Mono Lake	4	0.5560333
Mono Lake	5	0.6631000
Mono Lake	6	0.5484000
Mono Lake	7	0.3518667
Mono Lake	8	0.4315667
Mono Lake	9	0.9013667
Mono Lake	10	0.8890333
Mono Lake	14	0.3681667
Mono Lake	16	0.8227667
Mono Lake	18	0.5188000
Mono Lake	19	0.8930667
Mono Lake	20	0.4240000